

## TAXONOMIC AND NOMENCLATURAL COMMENTS ON THE TRITICEAE IN NORTH AMERICA

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### ABSTRACT

Miscellaneous information concerning the Triticeae in North America is presented. New combinations are provided for three subspecies of *Elymus elymoides*, one subspecies of *Leymus mollis*, two species of *Thinopyrum*, and four intergeneric hybrids. *Agropyron* is described as a well-circumscribed genus, whose treatment at the species level in North America is complicated by human manipulation. *Elymus* is interpreted as including *E. repens*, the type species of *Elytrigia*. A description of *Thinopyrum* is provided and the genus expanded to include two introduced species sometimes included in *Agropyron* or *Elytrigia*. Evidence suggesting that *Elymus californicus* should be transferred to *Leymus* is reviewed. Finally, a list of several unpublished theses involving systematic research on North American Triticeae is given.

**KEY WORDS:** *Agropyron*, *Elymus elymoides*, *Elymus repens*, *Elymus stebbinsii*, *Thinopyrum*,  $\times$  *Elyhordeum pilosilemma*, North America, taxonomy, nomenclature, Triticeae, Poaceae

### INTRODUCTION

This paper presents miscellaneous matters concerning the treatment of the Triticeae in the forthcoming *Manual for Grasses of the Continental United States and Canada* (Barkworth *et al.*, in prep.). The items included are: taxonomic treatment of *Agropyron*, *Elytrigia*, *Thinopyrum*, and *Leymus*, valid publication of names for the infraspecific taxa of *Elymus elymoides*, comments on recent findings concerning *Elymus stebbinsii* and *Elymus californicus*, and transfer of  $\times$  *Agrohordeum pilosilemma* to  $\times$  *Elyhordeum pilosilemma*. The items are treated in the above order. Illustrations of all the taxa will be included in the Manual.

*Agropyron*

One of the few points of agreement concerning the generic treatment of perennial Triticeae is that *Agropyron* Gaertner should be restricted to the "crested wheatgrasses". Starting in the nineteenth century, the departments of agriculture in the United States and Canada have been bringing accessions of *Agropyron* into North America, looking for grasses that would increase the grazing potential of arid regions in the west. These accessions were planted in experiment stations where they became the focus of breeding programs designed to develop cultivars appropriate to different parts of the continent. These programs included controlled and uncontrolled hybridization and attempts to increase the fertility of sterile hybrids by artificially doubling their chromosome complement and selecting for the most fertile offspring.

The result is a taxonomic dilemma. As Dewey stated (1986), "... taxa introduced into North America soon lose their taxonomic identity and genetic integrity because of extensive intercrossing that occurs in nursery situations where many accessions are grown in close proximity to each other", and "[many North American introductions] are genetically mixed by hybridization and single accessions often contain several morphological forms" (*ibid.*, p. 38). After careful consideration of specimens, including type specimens, at LE (herbarium codes from Holmgren *et al.* 1990) as well as North American plant material, Dewey concluded that the best solution was to treat North American material as belonging to one of three species, *Agropyron cristatum* (L.) Gaertner, *A. desertorum* (Fischer *ex* Link) Schultes, or *A. fragile* (Roth) P. Candargy. He summarized their distinguishing characters in a table (Table 1). He also stated, however, that "Classification of crested wheatgrass accessions or individual plants into one of the three species will often be difficult and unsatisfying".

I wholeheartedly agree with the last statement. Unfortunately, because crested wheatgrass has been widely planted on rangelands in arid regions of North America, taxonomists are often asked to identify it. I generally try to persuade those asking for identifications to be happy with *Agropyron* sp. If a binomial is required, Dewey's approach is practical, albeit artificial. Providing names at a lower taxonomic rank would require a better understanding than I have of the variation in *Agropyron* in Eurasia and an examination of the numerous type specimens involved. It seems best to let sleeping dogs lie. *Agropyron* in North America should be considered an example of human-induced despeciation.

*Elytrigia* and *Thinopyrum*

In the past, Tsvelev (1976), Löve (1984), Dewey (1984), and Barkworth (1989) included *Elymus repens* in *Elytrigia*, of which it is the type species. According to Tsvelev (1976), *Elytrigia* differed from *Elymus* in having completely sessile spikelets, a tardily or non-disarticulating rachilla, and glumes that were scabrous only on the midrib, had a transverse indentation near the base and well developed keel towards the tip. He included in the genus species that Dewey (1984) and Barkworth (1989) treated in *Pseudoroegneria* or *Thinopyrum*.

A major factor in Dewey's and my decisions was the observation that Tsvelev's treatment of the Triticeae tended to concur with relationships suggested by cytogenetic

data and Tsvelev's knowledge of a wide range of Triticeae. Others prefer to include the species, and Tsvelev's other species of *Elytrigia*, in *Elymus* (e.g., Melderis 1978; Cope 1982). Melderis, in explaining his decision, cited the morphological continuity between segregate genera such as *Pseudoroegneria*, *Elymus*, *Elytrigia*, and *Thinopyrum* and the frequency with which hybrids between these genera occur.

Despite my treatment of *Elymus repens* as a species of *Elytrigia*, I recognized that its overall appearance, if one excludes the rhizomatous character, is similar to that of other species of *Elymus*. I admit, however, that my decision to include *Elymus repens* in *Elymus* was made when it was discovered that it is genomically similar to other species of *Elymus* (Assadi & Runemark 1995). Genomic constitution, by itself, should not determine the generic placement of a species, but if other data have one sitting on the fence (a position that is not evident from one's nomenclatural practice), a single character may have more apparent importance than would otherwise be the case.

*Elymus repens* differs from most species occurring in North America in being a hexaploid with a genomic composition of StStH (genomic symbols are based on recommendations in Wang *et al.* 1996). *Elymus transhyrcanus* Tsvelev, a Transcaucasian and central Asian species, is the only other StStH species known (Dewey 1972), but there are many species of Triticeae for which the genomic composition is not yet known.

The inclusion of *Elymus repens* in *Elymus* raises the question of how to treat other species that have been included in *Elytrigia*. Melderis (1978) and Assadi & Runemark (1995) include them in *Elymus*, but I prefer to continue recognizing both *Thinopyrum* *sensu* D.R. Dewey (1986) and *Pseudoroegneria* (Carlson & Barkworth 1998). This made it necessary to review the two other species of *Elytrigia* reported from North America, *Elytrigia pungens* (Pers.) Tutin and *Elytrigia pycnantha* (Godron) A. Löve.

*Thinopyrum* consists of species with solitary, trullate spikelets with stiff, thick, acute to truncate glumes, tardily or non-disarticulating rachillas, and long anthers. Both *Elytrigia pungens* and *Elytrigia pycnantha* species, but not *Elymus repens* fall within this circumscription. I therefore propose the following combinations:

***Thinopyrum pungens* (Pers.) Barkworth, *comb. nov.* BASIONYM:** *Triticum pungens* Pers., *Syn. Pl.* 1:109 (1805).

SYNONYMS: *Agropyron pungens* (Pers.) Roemer & Schultes, *Syst. Veg.* 2:753 (1817); *Elytrigia pungens* (Pers.) Tutin, *Watsonia* 2:186 (1952); *Elymus pungens* (Pers.) Melderis, *Bot. J. Linn. Soc.* 76:380 (1978); *Psammopyrum pungens* (Pers.) A. Löve, *Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich* 87:50 (1986).

***Thinopyrum pycnanthum* (Godron) Barkworth, *comb. nov.* BASIONYM:** *Triticum pycnanthum* Godron, *Mém. Soc. Emul. Doubs., sér. 2*, 5:10 (1854).

SYNONYMS: *Agropyron pycnanthum* (Godron) Gren. in Gren. & Godron, *Fl. France* 3:606 (1856); *Elymus pycnanthus* (Godron) Melderis, *Bot. J. Linn. Soc.* 76:378 (1978); *Elytrigia pycnantha* (Godron) A. Löve, *Taxon* 29:351 (1980).

*Triticum litorale* Host, *Icones Descr. Gram. Austriac.* 4:5 (1809), *non* Pallas (1773); *Triticum pungens* auct., *non* Pers. (1895); *Agropyron pungens* auct., *non* Roemer & Schultes (1817).

Table 1. Comparison of *Agropyron fragile*, *A. desertorum*, and *A. cristatum* sensu lato, based on Tsvelev (1976), Dewey (1986), and personal observation.

Character	<i>A. fragile</i>	<i>A. desertorum</i>	<i>A. cristatum</i>
Spike length	3-15 cm	2-7 cm	(1.5)2-6(8) cm
Spike width	0.5-1 cm	0.5-1 cm	0.8-2.3 cm
Spike shape	Linear	Narrowly lanceolate to oblong or broadly linear	Oblong to broadly oblong
Spikelets (below midlength)	Appressed or diverging at an angle of less than 30°	Diverging at an angle of 25-45°	Diverging at an angle of 45-90°
Glumes	Appressed to lemmas	Appressed to lemmas	Not appressed to lemmas
Lemma apex	Unawned, sometimes with a mucro up to 1 mm long	With an awn 1-4 mm long	With an awn up to 5 mm long

Neither species has been studied genomically, but Assadi & Runemark (1995, p. 201) state that "[they] obviously have a J, with the other genomes not yet satisfactorily determined". All species of *Thinopyrum* for which the information is available have at least one copy of this genome (or its variant, the J<sup>\*</sup> genome), sometimes in combination with other genomes (Assadi & Runemark 1995).

### *Elymus elymoides*

*Elymus elymoides* (Raf.) Swezey is sometimes included in *Sitanion* (Hitchcock 1951; Clayton & Renvoize 1986). Species of *Sitanion* differ from other species of *Elymus* primarily in their disarticulating rachis and the long, arcuately diverging awns of their glumes and lemmas. This combination of characters promotes wind dispersal of the diaspores over open, relatively bare ground. *Sitanion* was last revised by Wilson (1963) but, in my treatment for the Jepson Manual (Barkworth 1993), I followed Holmgren & Holmgren (1977) in recognizing two species, one with four infraspecific taxa, but chose to include the species in *Elymus* and treat the infraspecific taxa as subspecies rather than varieties. Unfortunately, I managed to overlook the need to publish the new combinations. They are presented here for the first time:

*Elymus elymoides* (Raf.) Swezey subsp. *brevifolius* (J.G. Sm.) Barkworth, comb. nov. BASIONYM: *Sitanion brevifolium* J.G. Sm., Bull. U.S.D.A. Div.

Agrostol. Rep. Agrostol. 18:17 (1899). HOLOTYPE: United States. Arizona: Pima County, Tucson, 1892, *Toumey* 797 (US).

*Elymus elymoides* (Raf.) Swezey subsp. *californicus* (J.G. Sm.) Barkworth, *comb. nov.* BASIONYM: *Sitanion californicum* J.G. Sm., Bull. U.S.D.A. Div. Agrostol. Rep. Agrostol. 18:13 (1899). TYPE: United States. California: San Bernardino County, San Bernardino Mountains, 23 June 1894, *Parish* 3295 (US).

*Elymus elymoides* (Raf.) Swezey subsp. *hordeoides* (Suksd.) Barkworth, *comb. nov.* BASIONYM: *Sitanion hordeoides* Suksd., Werdenda 1:4 (1923). HOLOTYPE: United States. Washington: Spokane County, Spangle, 29 June 1916, *Suksdorf* 8705 (WS).

### *Elymus stebbinsii*

As Michael Curto drew to my attention (oral comm. 1993), the holotype of *Agropyron parishii* Scribner & J.G. Smith var. *laeve* Scribner & J.G. Smith belongs in *Elymus trachycaulus* (Link) Gould subsp. *subsecundus* (Link) Gould. This means that names based on *A. parishii* var. *laeve* are synonyms of *E. trachycaulus* subsp. *subsecundus* and raised the question as to whether there is a taxon corresponding to the description of Scribner & Smith. After studying specimens from several herbaria, (Barkworth 1998) I concluded that there is such a taxon and named it *E. stebbinsii* Gould subsp. *septentrionalis*. It grows to the north and east of the Great Central Valley of California, not in San Diego County where the holotype of *Agropyron parishii* var. *laeve* was collected.

### *Elymus californicus*

*Elymus californicus* (Bol.) Gould has traditionally been included in *Hystrix* as *H. californica* Bol. Inclusion of the type species for *Hystrix*, *H. panula* Moench [= *E. hystrix* L.] in *Elymus* meant that the generic placement of *H. californica* had to be reconsidered. In preparing the treatment of *Elymus* for the Jepson Manual (Barkworth 1993), I did not examine either species closely, largely because I was unaware of any compelling reasons for believing that they did not belong in *Elymus*. In particular, the general aspect and habitat of *E. californicus* seemed compatible with its inclusion in *Elymus*, if that genus included *E. hystrix* and *E. svensonii* G.L. Church. The only discordant note was Stebbins' (cited in Myers 1947) report that it was an octoploid, making it the only known octoploid in *Elymus* so far as I am aware. Löve (1980) initially reported that it had  $2n = 28$ , as is typical of North American species of *Elymus*, but later (Löve 1984), without comment, listed only  $2n = 56$ . More recently, Dr. Kevin Jensen (pers. comm., 1997) confirmed Stebbins count of  $2n = 56$ .

Dewey (1983) considered *Elymus hystrix* an StH tetraploid, like most North American species of *Elymus*. He presented no direct evidence for this statement. The only cytological information for the species came from Church's (1967) crosses of *E. hystrix* with other eastern North American species of *Elymus*. Most of the crosses were unsuccessful, but a few yielded partially fertile hybrids. The most successful crosses were with *E. svensonii*. Unfortunately, *E. svensonii* is another genomically uncharacterized species.



Svitashev *et al.* (1997), using genome-specific repetitive DNA and RAPD markers, confirmed the presence of the H genome in *Elymus hystrix*, but only one of their three St genome-specific primers supported the presence of the St genome. They suggested that the St genome in *E. hystrix* may be substantially modified from that found in the other species of *Elymus* that they examined. They did not examine *Hystrix californica*, but did include two other species traditionally placed in *Hystrix*, *H. duthei* (Stapf) Bor and *H. komarovii* (Roshev.) Ohwi. Both responded to the markers used like the species of *Leymus* included in the study, not like unusual StH species.

Other studies also suggest that many species traditionally included in *Hystrix* are closer to *Leymus* than *Elymus*. Jensen & Wang (1997) transferred *H. coreana* (Honda) Ohwi to *Leymus* because both their cytological and molecular data (genome-specific RAPD markers) suggested that it belonged there. Their molecular data also supported transferring *H. californica*, but they left it in *Elymus* pending acquisition of cytological data. They did not comment on the morphology or ecology of either taxon, nor did they include *H. patula* in their study.

Baden *et al.* (1997) recognized *Hystrix* in the traditional sense. They argued that a) genomic information is of dubious value in phylogenetic analysis and b) that *Elymus* is undoubtedly polyphyletic so that removal of morphologically distinct groups would contribute to a better understanding of its relationships. They describe *Hystrix* as consisting of "loosely tufted species and though difficult to circumscribe precisely, the following combination of character states appears to set [*Hystrix*] apart from all other species of Triticeae 1) glumes either absent or reduced to tubercles or if present setaceous or subulate with carinate base (never flat), free, distinctly unequal, and inconspicuously 1(3)-nerved, never longer than the lemma (including awn), 2) large anthers (>2.5 mm), 3) spikelets disarticulating below the lowermost floret, and 4) lemma 4-7-nerved" (p. 450).

Of the six species that they recognized, three (*Hystrix patula*, *H. coreana*, and *H. sibirica* [Trautv.] Kuntze) had linear to broadly lanceolate leaves, the other three (*H. californica*, *H. duthei* [Stapf] Bor, and *H. komarovii* [Roshev.] Ohwi) having broad, lanceolate leaves. C-banding patterns for *H. patula*, *H. komarovii*, and *H. duthei* were distinct from those for *H. coreana*. The habitat summaries suggest that *H. coreana* and *H. sibirica* grow in rather open, rocky or sandy environments whereas the other four species grow in shadier locations within a forest and that *H. californica* and *H. duthei* tend to flower earlier in the season than the other four species.

The authors did not comment on *Elymus svensonii*, but it appears to fit the morphological criteria for *Hystrix*, nor did they provide any evidence that *Hystrix*, as they circumscribed it, is a monophyletic taxon. While genomic data cannot be used, by themselves, to determine the phylogenetic relationships among polyploid taxa, Svitashev *et al.* (1996) showed that they may be phylogenetically informative. At present, cytological and molecular data suggest that *Hystrix*, as recognized by Baden *et al.* (1997), is polyphyletic.

Because *Elymus hystrix* is the type species for *Hystrix*, its inclusion in *Elymus* precludes returning *E. californicus* to that genus. One could retain *E. hystrix* in *Hystrix*, as Baden *et al.* advocate, but one should then reconsider the generic affiliation

of *E. svenssonii* and *E. diversiglumis* Scribner & C.R. Ball. I believe that all three are best included in *Elymus*, but I am not completely convinced that *E. californicus* belongs there. On the other hand, I am not happy about transferring it to *Leymus* because it is so ecologically and morphologically distinct from that genus as I know it (Barkworth & Atkins 1984). My knowledge does not, however, include the Asian and South American species that Jensen & Wang (1997) and Dubcovsky *et al.* (1997) recently transferred to *Leymus*, nor am I familiar with the Asian species traditionally included in *Hystrix*. It seems best, therefore to leave *E. californicus* in *Elymus* pending more complete and multidisciplinary data on all the relevant species. The reason for this note is to draw attention to the anomalous aspects of *E. californicus* and to correct my report (Barkworth 1993) of an incorrect chromosome count for *E. californicus*.

### *Elymus glaucus*

No nomenclatural changes are proposed for *Elymus glaucus* Buckley, but specimens examined as part of the study of *E. stebbinsii* (Barkworth 1998), indicated that anther length ranges from 2.0–4.6 mm in the species. I reexamined specimens at both extremes, but finally concluded that the upper limit had to be increased over the value I gave earlier (Barkworth 1993). I also found variation within individual specimens, in one case finding anthers of 3.6 and 4.6 mm on the same plant. Plants with shorter anthers showed less absolute variation. Snyder (1950) published a landmark paper on morphological variability in *E. glaucus*, but anther length was not one of the characters he studied.

### Intergeneric Hybrids

The Triticeae is notorious for the ability of its members to hybridize, even between genera. Most of the intergeneric hybrids are highly sterile and very local in their distribution, but many have been given binomial names. The new combinations will permit the application of generic concepts adopted in the *Manual* to named, naturally occurring North American hybrids.

× *Elyhordeum californicum* (Bowden) Barkworth, *comb. nov.* BASIONYM:

*Sitordeum californicum* Bowden, *Canad. J. Bot.* 45:722 (1967). SYNONYM: × *Elytesion californicum* (Bowden) Barkworth & D.R. Dewey, *Amer. J. Bot.* 72:772 (1985). Parents: *Sitanion jubatum* J.G. Sm. [= *Elymus multisetus* (J.G. Sm.) M.E. Jones] and *Hordeum jubatum* L.

× *Elyhordeum pilosilemma* (W.W. Mitchell & H.J. Hodgson) Barkworth, *comb.*

*nov.* BASIONYM: × *Agrohordeum pilosilemma* W.W. Mitchell & H.J. Hodgson, *Bull. Torrey Bot. Club* 92:404 (1965). Parents: *Elymus macrourus* (Turcz.) Tzvelev [= *Agropyron sericeum* Hitchc.] and *Hordeum jubatum* L.

× *Leydeum* Barkworth, *gen. hybr. nov.*, *Leymus* Hochst. × *Hordeum* L.

- × *Leydeum dutillyanum* (Lepage) Barkworth, *comb. nov.* BASIONYM: × *Elymordeum dutillyanum* Lepage, *Naturaliste Canad.* 84:97 (1957). Synonym: × *Leytesion dutillyanum* (Lepage) Barkworth in Barkworth & R.J. Atkins, *Amer. J. Bot.* 71:623 (1984). Parents: *Leymus mollis* (Trin.) Pilger and *Hordeum jubatum* L.
- × *Leydeum piperi* (Bowden) Barkworth, *comb. nov.* BASIONYM: × *Elymordeum piperi* Bowden, *Canad. J. Bot.* 36:106-107 (1958). Parents: *Leymus triticoides* (Buckley) Pilger and *Hordeum jubatum* L.

## UNPUBLISHED THESES

In working with North American Triticeae, some unpublished theses and dissertations have come to my attention. Because they contain useful information, I am listing them here so that others working on the tribe may locate them. In most cases, the reason that no publication resulted from the work is that publication was not necessary for the student's career after graduation. A few are available through UMI®; the remainder are, presumably, deposited in the libraries of the institutions concerned. The Intermountain Herbarium also has a copy of each. I would welcome information on additional unpublished theses and dissertations concerning the tribe.

- Brooks, R.E. Intraspecific variation in *Elymus virginicus* (Gramineae) in the central United States. M.A. thesis, University of Kansas.
- Collins, D.D. 1965. Ecological, biosystematic, and biochemical studies of species in the genus *Agropyron* Gaertn. native to Montana. Ph.D. dissertation, Montana State College.
- Davies, R.S. 1980. Introgression between *Elymus canadensis* L. and *E. virginicus* L. (Triticeae, Poaceae) in south central United States. Ph.D. dissertation, Texas A&M University.
- Godley, E.J. 1947. The variation and cytology of the British species of *Agropyron* and their natural hybrids. M.Sc. thesis, Cambridge University, United Kingdom.
- Jensen, Jr., E.R. 1972. A taxonomic study of single spikelet *Elymus* species of western North America. Ph.D. dissertation, Utah State University.
- Jozwik, F.X. 1966. A biosystematic study of the slender wheatgrass complex. Ph.D. dissertation, University of Wyoming.

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## LITERATURE CITED

- Assadi, M. & H. Runemark. 1995. Hybridization, genomic constitution and generic delimitation in *Elymus* s.l. (Poaceae, Triticeae). *Pl. Syst. Evol.* 194:189-205.
- Baden, C., S. Frederiksen, & O. Seberg. 1997. A taxonomic revision of the genus *Hystrix*. *Nordic J. Bot.* 17:449-467.
- Barkworth, M.E. 1989. Poaceae. Pp. 316-342 in R.J. Shaw, *Vascular Plants of Northern Utah*. Utah State University Press, Logan, Utah.
- Barkworth, M.E. 1993. *Elymus*. Pp. 1253-1256 in J.C. Hickman, *The Jepson Manual*. University of California Press, Berkeley, California.
- Barkworth, M.E. 1998. *Elymus stebbinsii*: taxonomy, nomenclature, and distribution. *Phytologia* 83:345-365.
- Carlson, J.R. & M.E. Barkworth. 1998. *Elymus wawawaiensis*: A species hitherto confused with *Pseudoroegneria spicata* (Triticeae, Poaceae). *Phytologia* 83:312-330.
- Church, G.L. 1967. Taxonomic and genetic relationships of eastern North American species of *Elymus* with setaceous glumes. *Rhodora* 69:121-162.
- Clayton, W.D. & S.A. Renvoize. 1986. *Genera Graminum*. Her Majesty's Stationery Office, London, United Kingdom.
- Cope, T.A. 1982. Poaceae, vol. 143 in E. Nasir & S.I. Ali (Eds.), *Flora of Pakistan*. Department of Botany, University of Karachi, Pakistan.
- Dewey, D.R. 1972. The origin of *Agropyron leptourum* [= *Elymus transhyrcanus* (Nevski) Tzvelev]. *Amer. J. Bot.* 59:836-842.
- Dewey, D.R. 1983. Historical and current taxonomic perspectives of *Agropyron*, *Elymus*, and related genera. *Crop Sc.* 23:637-642.
- Dewey, D.R. 1984. The genomic system of classification as a guide to intergeneric hybridization in the perennial Triticeae. Pp. 209-279 in J.P. Gustafson (Ed.), *Gene Manipulation in Plant Improvement*. Plenum Publishing Corporation, New York, New York.
- Dewey, D.R. 1986. Taxonomy of the crested wheatgrasses. Pp. 31-44 in K.L. Johnson (Ed.), *Crested wheatgrass: its values, problems, and myths*. Proceedings of a symposium, held in 1983 at Utah State University, Logan, Utah.
- Dubcovsky, J., A.R. Schlatter, & M. Echaide. 1997. Genome analysis of South American *Elymus* (Triticeae) and *Leymus* (Triticeae) species based on variation in repeated nucleotide sequences. *Genome* 40:505-520.
- Hitchcock, A.S. 1951. *Manual of Grasses of the United States*, edition 2, revised by A. Chase. U.S.D.A. Misc. Publ. No. 200. U.S. Government Printing Office, Washington, D.C.
- Holmgren, A.H. & N.H. Holmgren. 1977. *Sitanion*. Pp. 306-310 in A. Cronquist et al., *Intermountain Flora*. Columbia University Press, New York, New York.
- Holmgren, P.K., N.H. Holmgren, & L.C. Barnett. 1990. *Index Herbariorum*. Part 1: The herbaria of the world. International Association for Plant Taxonomy, New York Botanical Garden, Bronx, New York.
- Jensen, K.B. & R.R.-C. Wang. 1997. Cytological and molecular evidence for transferring *Elymus coreanus* from the genus *Elymus* to *Leymus* and molecular evidence for *E. californicus* (Poaceae: Triticeae). *Int. J. Pl. Sc.* 158:872-877.

- Löve, A. 1980. Poaceae-Triticeae americanae. Pp. 166-169 in A. Löve, IOPB Chromosome number reports 66. *Taxon* 29:163-169.
- Löve, A. 1984. Conspectus of the Triticeae. *Feddes Repert.* 95:425-526.
- Melderis, A. 1978. Taxonomic notes on the tribe Triticeae (Gramineae) with special reference to the genera *Elymus* L. sensu lato, and *Agropyron* Gaertner sensu lato. *Bot. J. Linn. Soc.* 76:369-384.
- Myers, W.M. 1947. Cytology and genetics of forage grasses. *Bot. Rev. (Lancaster)* 13:319-421.
- Snyder, L.A. 1950. Morphological variability and hybrid development in *Elymus glaucus*. *Amer. J. Bot.* 37:628-636.
- Svitashev, S., B. Salomon, A. Vershinin, C. Pedersen, T. Säll, & R. von Bothmer. 1996. A study of 28 *Elymus* species using repetitive DNA sequences. *Genome* 39:1093-1101.
- Svitashev, S., T. Bryngelsson, X. Li, & R.R.-C. Wang. 1997. Genome-specific repetitive DNA and RAPD markers for genome identification in *Elymus* and *Hordelymus*. Paper 4 in Ph.D. dissertation by S. Svitashev, Swedish University of Agricultural Sciences, Svalöv, Sweden.
- Tsvelev, N.N. 1976. *Zlaki SSSR [Grasses of the U.S.S.R.]*. Nauka, Leningrad, U.S.S.R.
- Wang, R.R.-C., R. von Bothmer, J. Dvorak, G. Fedak, I. Linde-Laursen, & M. Muramatsu. 1996. Genome symbols in the Triticeae (Poaceae). Pp. 29-34 in R.R.-C. Wang, K.B. Jensen, & C. Jaussi, (Eds), *Proc. Second International Triticeae Symposium. Forage and Range Laboratory, U.S.D.A.-A.R.S., Logan, Utah*. (See also <http://www.biology.usu.edu/herbarium/triticeae/gensymb.html>).
- Wilson, F.D. 1963. Revision of *Sitanion* (Triticeae, Gramineae). *Brittonia* 15:303-323.